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GEOTACTIC BEHAVIOUR OF *DREISSENA POLYMORPHA* (BIVALVIA)

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ABSTRACT

Zebra mussel movement was studied in the laboratory, on a glass slope inclined at 2, 3, 4 or 8° to the bottom, in darkness and in the light (the latter on the steepest slope only). Small mussels (< 10 mm) climbed upward on the 4 or 8° slopes in darkness (negative geotaxis) but showed no preferences on the other slopes and in the light. Large mussels (> 12 mm) moved downwards on the 4 and 8° slopes (also in the light) and showed no preferences in the other treatments.

INTRODUCTION

Dreissena polymorpha (Pallas, 1771), the zebra mussel, is a gregarious bivalve that strongly influences freshwater ecosystems and hydrotechnical devices (Lewandowski, 2001; O'Neill, 1997). Its distribution is mainly determined by dispersal and settlement of planktonic larvae (Lewandowski, 2001; Kobak, 2004), but may also be affected by post-settlement movement of mussels: they move upwards to avoid poor chemical conditions at the base of a colony (Burks et al., 2002) and prefer shaded or dark substrata (Kobak, 2001; Toomey et al., 2002).

A cue that could be useful for a moving mussel is gravity. It provides information to an animal about its orientation in space, independent of photoperiod and geographic location. In the field, zebra mussels may prefer either the lower (Walz, 1973; Lewandowski, 2001) or upper (Marsden & Lansky, 2000) substrate side. Such distribution could result from both geo- and phototaxis, as well as the effects of water flow or predation. To test the influence of gravity upon mussels, I studied their movement on a series of slopes in the laboratory. In the light of my field research (Kobak, 2004), I hypothesized that small mussels would move upwards and illumination would reverse this behaviour because of negative phototaxis. I also expected that large mussels, less mobile than small ones, would prefer the easier, downward direction.

MATERIALS AND METHODS

Mussels were collected by a diver from a dam wall of the Włocławek Dam Reservoir (the Vistula River, central Poland) and kept in a 500 l aquarium filled with aerated, settled tap water, at ca. 20°C. Only individuals that reattached themselves in this aquarium were tested. They were used only once, not sooner than two weeks and not later than three months after collecting. The tested individuals were divided into small mussels (mean shell length ± SD: 7.3 ± 1.29 mm, range: 3.3–9.9 mm) and large ones (15.3 ± 1.55 mm, range: 12.2–22.6 mm).

The experiment was run in a glass tank (480 x 230 mm, water level: 240 mm) with settled (24 h) tap water (19–22.5°C). A 400 x 230 mm glass plate was put into the tank, with one of its longer edges resting on the bottom and the other leaning against the wall (Fig. 1). The aerator was placed below the plate level to avoid mussel disturbance by air bubbles. The mussels (13 individuals per tank in a single trial) were put onto the central long axis of the plate, with their long axes parallel to the tank's longer edge. Each mussel was covered with a glass tunnel (width and height: 25 mm, length: 220 mm, outlets closed with 1 mm nylon mesh) to avoid the impact of conspecifics on their behaviour (Mörtl & Rothhaupt, 2003).

To study geotaxis in the dark, I tested mussels on slopes inclined at 2, 3, 4 or 8° to the bottom, in a tank covered with a cardboard

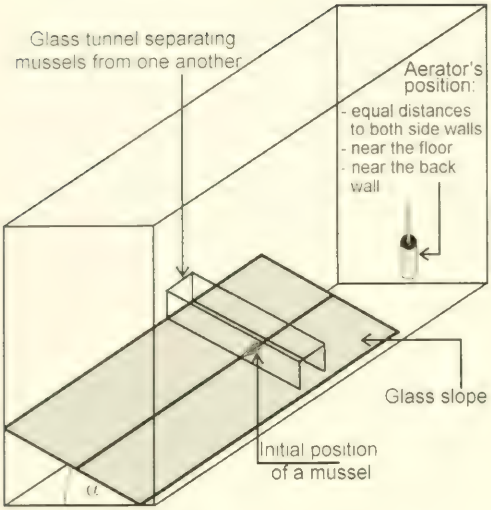
Glass tunnel separating mussels from one another
Aerator's position:
- equal distances to both side walls
- near the floor
- near the back wall
Glass slope
Initial position of a mussel
α

FIG. 1. Experimental tank. α in various treatments is 2. 3. 4 or 8°.

box. Illumination under this box was below the detection limits of the luxometer (Sonopan L-20A) (i.e., < 0.1 lx). To examine the impact of light on geotaxis, I tested mussels on a constantly illuminated slope (16 W bulb 0.5 m above the surface, incident illuminance at the surface ca. 700 lx). Light was used only in experiments involving the steepest slope (8°), the most likely to evoke geotaxis.

To check whether mussels could passively slide down the slope, 20 empty shells of each size group, filled with aquarium silicon glue to imitate a live mussel's shape and weight, were put on the steepest slope (8°) in various positions (lying on the ventral or side shell surface, with the front, back, or side pointing down). I observed no passive relocations of these shells.

I carried out ten 48-hour trials (13 mussels in each) for each treatment and size group. They were run consecutively, in a random sequence. The slope direction relative to the laboratory room was changed in the successive trials. At the end of each trial, distances moved by the mussels (measured to their anterior ends) were determined to the nearest 1 cm (the scores were from -11 at the bottom to +11 at the top).

Numbers of mussels moving in opposite directions were compared using t-tests for paired data with the sequential Bonferroni correction.

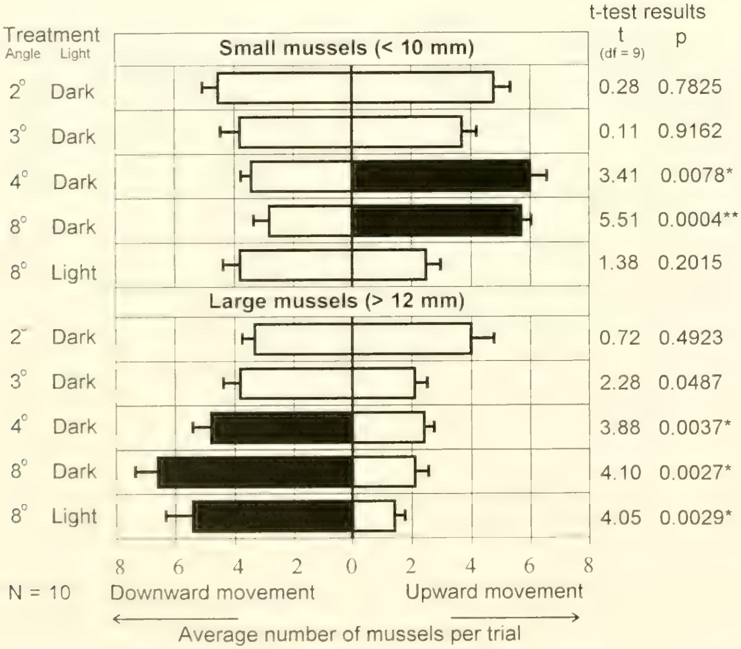

FIG. 2. Direction of zebra mussel movement on different slopes. Error bars are standard errors of mean. Black bars indicate a significant preference for one direction in a given treatment. The asterisks show statistical significance of the t-tests for paired data after applying the sequential Bonferroni correction: $^*p < 0.05$, $^{**}p < 0.01$.

Differences among the treatments were tested using the two-way ANOVA (factors: mussel size and slope type) of individual distances moved by the mussels (with downward distances coded as negative values). The Bonferroni-adjusted pairwise t-tests were used as post-hoc comparisons. Mussels that neither moved nor attached themselves to the plate were regarded as being in a poor physical condition and not analysed.

RESULTS

On the darkened 4 and 8° slopes, the small mussels tended to move upwards, while the large individuals preferred the downward direction. In the light preferences of the small mussels disappeared, while the large ones retained their downward preference. I observed no directional reactions on the other slopes (Fig. 2).

The interaction between mussel size and slope was significant in the ANOVA of the distances ($F_{4,\ 1014} = 7.97$, $p < 0.001$). The distances moved by the small mussels on the darkened 4 and 8° slopes differed significantly from those measured in the other treatments, as well as from the distances moved by the large individuals in the same conditions. In the case of the large mussels, only the distances moved on the 2 and 8° slopes differed significantly from each other (Fig. 3).

DISCUSSION

To my knowledge, negative geotaxis of metamorphosed bivalves has not been reported so far. Uryu et al. (1996) observed positive geotaxis of a mussel *Limnoperna fortunei*. Negative geotaxis of small zebra mussels, found here, could account for the aggregations of recruits along the upper edge of vertical settlement plates deployed in the field (Kobak, 2004).

Negative geotaxis could be beneficial in a dense colony, where water quality is poor. Burks et al. (2002) found an upward movement of mussels apparently stimulated by chemical gradients within a colony (e.g., oxygen and nitrate). In the present study, mussels moved upwards, although they were kept at low density and separated from one another, so such a gradient did not appear. Thus, in certain conditions, upward movement may occur without any chemical stimuli. In the field, negative geotaxis could help mussels to find a suitable site at the top of a colony. However, zebra mussels are photophobic (Kobak, 2001; Toomey et al., 2002), which is contradictory to negative geotaxis: climbing up means approaching the light source. Photophobic behaviour may explain why the upward movement of small mussels disappeared under illumination in the present study. Uryu et al. (1996) observed a light-induced change in

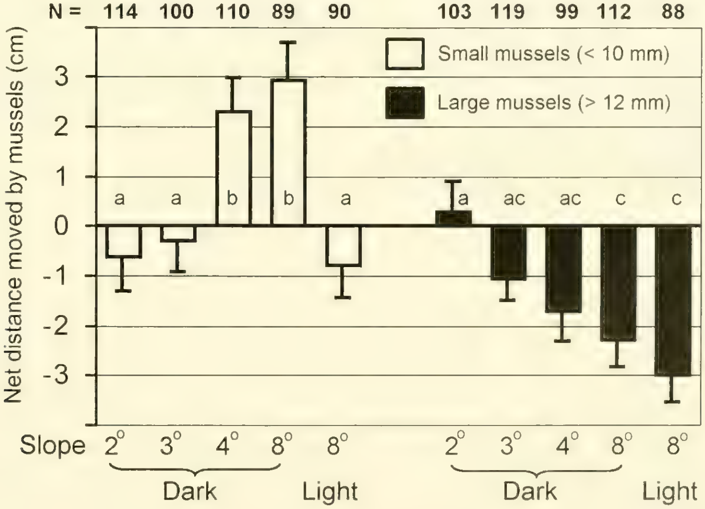

FIG. 3. Average net distances moved by zebra mussels on different slopes. Downward distances were counted as negative values. Treatments labelled with the same letter did not differ significantly from one another (Bonferroni-adjusted t-tests). The values above the chart are the numbers of mussels analysed in each treatment.

behaviour of *L. fortunei*, which chose no direction in darkness and moved downwards in light. For both species, illumination reduced upward movement. Previously, I have shown that light (ca. 700 lx) was a stronger cue than gravity: small mussels avoided the upper, illuminated part of the slope when only its lower half was darkened (Kobak, 2002).

Large mussels move less frequently and over shorter distances than smaller mussels, probably due to their heavier bodies (Toomey et al., 2002). Thus, larger individuals may prefer the downward direction because it demands less effort. Older mussels often bear other individuals attached to their shells, which further limits their locomotion and makes it less likely to be crucial to their survival.

A number of studies (e.g., Kobak, 2001, 2002; Burks et al., 2002; Toomey et al., 2002), including the present one, show that small zebra mussels can use multiple environmental cues to select an attachment site by crawling over substratum. Thus, active movement of settled individuals may be an important factor affecting mussel distribution in the field.

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